SYNOPSIS OF THE TABANIDÆ OF NEW YORK, THEIR BIOLOGY AND TAXONOMY

I. The Genus Chrysops Meigen

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INTRODUCTION AND ACKNOWLEDGMENTS

This paper was begun in 1931. The work, as then outlined, was to consist of a study of the extensive literature on the family, a study of the insects in the field and in the collection, and life history studies of the species most common in the vicinity of Rochester.

In conformity with the first part of the work program, more than one hundred papers on Tabanidæ in English, German, and Russian were studied. Thanks are due to many authors who sent me reprints of their works, especially to Dr. Von O. Kröber (Hamburg) for authorization to adapt his classification of Chrysops.

The insect collection of the University of Rochester contains all the species of New York State, most of them identified by Johannsen. These were thoroughly studied from the anatomical and taxonomical aspects. Several visits were also made to Cornell University for the purpose of studying the Tabanidæ in the collection of the College of Agriculture. To Dr. J. Chester Bradley, curator of the insect collection, I am indebted for a liberal loan of many specimens representing species not available for study in our collection.

The vicinity of Rochester affords many ideal places for the study of Tabanidæ in nature. Durand-Eastman Park, situated on Lake Ontario, with its three ponds and swampy, wooded areas, is an excellent breeding ground for the flies. The many acres in the park devoted to the preservation of wild animal life, particularly deer and buffalo, offer plenty of food for the blood-sucking females. The swamps near Bergen, situated about twenty miles west of Rochester, are during the summer months dominated by

the horse-flies, particularly *Chrysops*. The swamps are surrounded by pasture lands where hundreds of cattle graze daily. The group of ponds known as Mendon Ponds near Rochester is also a favorable breeding place for horse-flies. There are wooded areas on the hills surrounding the ponds on one side and horse stables on the other side. The larger species of tabanids are particularly common in Mendon Ponds.

In the course of the study two species of *Chrysops, indus* and *obsoletus,* were reared from egg to adult. One species of *Tabanus* was likewise reared through all its stages. Many other species found as larvæ were observed in the laboratory in the course of their development into adults.

The attempt to study the embryology of some tabanids was unsuccessful due to the insoluble black pigment in the chorion of their eggs. The work will, however, be repeated in the coming season.

My studies were conducted in the entomological laboratory of the Department of Biology of the University of Rochester under the direction of Dr. J. Douglas Hood, without whose advice and guidance this work would have been impossible.

ECONOMIC IMPORTANCE AND CONTROL

Of all the Tabanidæ, *Chrysops* species most readily attack man. Many a specimen has been obtained by simply waving the net around the head. This affords a good protection from the bites of the flies and yields a large number of specimens in a comparatively short time. But then the collection will consist of females only, for they alone attack man and beast for the purpose of blood sucking.

The bite of the female is not very painful, but the continuous buzzing and pricking, particularly on the back of the neck and on the forehead, is extremely annoying. There seems to be a preference among the various species for certain specific parts of the host body. Some prefer the lobe of the ear, others the back of the hand, or various other exposed parts of the body. *Chrysops* species are not common on cattle, but they molest horses, and in the tropics they torture the elephant and the lion, and the reindeer, as well as man.

The puncture causes a small bleeding wound, but no pain is felt, except for a feeble twinge when the proboscis is withdrawn. No swelling results from the bite, and consequently no poison is conveyed into the wound by the piercing organs.

Some species of *Chrysops,* in common with other Tabanidæ, are mechanical transmitters of infectious diseases to man and animals. The nature of the transmission is not certain in all cases. Some are experimentally proven while others are based on circumstantial evidence. All the cases of disease transmission in which *Chrysops* species are involved or suspected of being involved are here discussed:

1. Tularæmia of man: This is an infectious disease due to *Bacterium tularense* which is transmitted to man by the bite of an infected blood-sucking fly or by handling infected rodents.

The blood-sucking fly which serves as the mechanical transmitter of the disease germ is *Chrysops discalis,* as proven by Francis and Mayne (1922). This species is very common in Utah, Colorado, Wyoming, and Washington. It has also been reported from other states of the Union. The disease is particularly common in rural districts among the field workers. The two conditions favorable for the spread of the disease are (1) the presence of infected rodents, and (2) the season of the fly's activity, which is June, July, and August, when farm labor is at its peak.

The disease is initiated by the bite of the fly on the face, neck, or exposed parts of hands or legs. The victim is not conscious of the bite; it is not painful. After the bite the infection sets in with fever and inflammation of the lymph glands in the vicinity of the bitten area. The illness is accompanied by a disability to do any work for two or three months. This means a loss in time and efficiency during the busiest season for the farmer. The virus, however, does not multiply inside the fly, and after five days of isolation the tendency to infect a healthy animal decreases.

2. *Loa loa:* This is a disease of man in tropical West Africa. It is caused by the parasitic nematode *Filaria loa* Guyot. Two species of Chrysops, *dimidiata* and *silacea,* have been demonstrated by Leiper (1913) and by the Connols (1922) to be concerned in the development and in the transmission of the parasite.

The embryos of the parasite pass through the mid-intestine of the fly and reach the thorax, where they remain coiled up in the thoracic muscles. On the twelfth day the development is complete and the embryos begin to travel towards the head, collect at the base of the proboscis, and pass into the hæmocœle in the labium. About 3.5 per cent of *Chrysops dimidiata* and *Chrysops silacea* are infected with the parasite in nature, and the two species are very common in the infested districts during May and June. The transmission is effected while biting the host. During that time the insect keeps on "milking" the labium with the forelegs, and the embryos rupture the walls of the labella and fall on the skin of the host. The embryos move rapidly, enter the skin, and in a very short time disappear beneath the surface.

3. In common with other Tabanidæ, species of Chrysops may be vectors of tsetse sickness of cattle, *Trypanosoma theileri* of sheep, *Trypanosoma evansi* (surra) of cattle, and *Trypanosome equinum* of the horse, and also in the transmission of swamp fever or infectious anemia of horses.

METHODS OF CONTROL

A. Biological Control.

I. Parasites on the eggs of Chrysops.

1. A minute hymenopteron, *Phanurus emersoni* Girault, belonging to the family Mymaridæ, is one of the most important parasites on the eggs of *Tabanidæ*. The female inserts the ovipositor into the chorion of the fly-egg where it deposits its eggs. Fresh egg-masses seem to be preferred to older ones, as it takes longer to puncture eggs over five or six hours old. About 93 per cent of all the egg-masses studied in Texas were found to be parasitized, and from six to 83 wasps emerged from each egg mass.

Investigators suggest a means of control by collecting the egg-masses and placing them in vessels along the river, these vessels being so constructed that they do not allow the parasite to escape, and serving to retain fly-larvæ inside later to be destroyed. A 50 per cent decrease in horseflies is reported in localities where parasite dissemination was supplemented by egg collecting.

2. *Phanurus tabanivorus* Ashmead has been reared from the eggs of several species of *Tabanidæ*.

3. *Trichogramma minutum* and other chalcids were reared in small numbers from eggs of Chrysops.

II. Parasites of Larvæ.

Larvæ are not open to successful attack because of their underground habitat. But there are several forms that feed on them.

1. Soon after hatching the young larvæ fall into the water where they molt prior to burrowing into the mud. At that time many are devoured by small fishes.

2. Jones and Bradley (1923) report *Phasiops flava* Coq. of the family Tachinidæ, and *Villa lateralis* Say of the family Bombyliidæ to be parasites on tabanid larvæ. They are also hosts to tachinid larvæ which eviscerate them.

3. Mature larvæ are sometimes infested by nematodes, particularly in the pre-pupal period.

4. Cannibalism reduces their number considerably.

III. Parasites of the Pupa.

Cameron and Philips report two Chalcids to be parasites of the pupa. They are *Trichopria tabanivora* Fauts and *Diglochis occidentalis* Ashmead.

IV. Parasites on Adults.

1. For about 30 minutes after emergence from the pupal case the flies are unable to fly as the wings are folded and are shorter than normal, and the abdomen is enlarged. At that time they fall an easy prey to predaceous Hemiptera, Odonata, and other insects.

2. Mites are often found on the bodies of the flies.

3. Birds capture the flies on the wing, and spiders entrap them in their nets and devour them.

4. The white-faced hornet (*Vaspa maculata* L.) has been observed to paralyze the fly and then dismember it by biting off the wings, the head and the abdomen, leaving only the thorax which is carried to the nest.

5. The horse-guard (*Monedula carolina* Drury), a predaceous wasp, is among the more important checks on the horsefly. These wasps lay their eggs in burrows and watch over them until they hatch. As soon as larvæ appear, the wasps supply them

with food, which consists of horsefly adults. The wasp frequents pastures where they pick the flies off the molested horses and cattle and carry them to their nests.

6. *Bembex,* another predaceous wasp, soars at about a man's height, and swoops down on the horsefly below, stings it, and paralyzes it immediately. It is then carried to the burrow as food for the young of the wasp.

Tabanidæ are said to be scarce where these wasps are present in great numbers, and their introduction is advocated as a means of control.

B. Physical Control.

By this term is meant the climatic and geographical factors that influence the increase or decrease of the flies.

1. Tabanids are most abundant after heavy rainfall in the summer. The breeding grounds are multiplied during such seasons. On the other hand such seasons are most unfavorable for the development of parasites, as they thrive in seasons of much sunshine.

2. Bodies of water and arboreal plants are the chief conditions for the existence and multiplication of horseflies. Where these conditions are absent Tabanidæ are scarce.

3. Tabanids favor the neighborhood of rivers, pools, and swamps, wooded areas and clearings, and the open roads in woodland.

C. Mechanical Control.

The mechanical means of control may be divided into three groups: (1) Repellents, (2) trapping, and (3) screens.

1. Several mixtures have been recommended for use as sprays and external applications, as well as for internal administration, for the purpose of repelling the flies. These consist of kerosene, tar-oils, and fish-oil emulsions for external use, and various salts for internal use.

None of these remedies has proved to be satisfactory preventives. Their effectiveness is of short duration and does not justify their high cost and labor. Many of these mixtures, besides being useless as far as relief is concerned, may be harmful to the hair and skin of the animals.

2. The habit of tabanids of flying frequently over the surface of water was utilized by the Russian entomologist Porchinsky to devise a method of trapping the flies in what he calls "pools of death." The pools most frequented by the flies are kept covered with a uniform layer of oils and the insect sticks to the surface of the water and perishes. Those that succeed in escaping perish subsequently since the oil spreads over the body causing suffocation by clogging the air passages.

This remedy was reported by Howard at the XIth meeting of the Association of Economic Entomologists in 1899. The limitations of the remedy were pointed out at the meeting, since only small, stagnant pools can be converted into "pools of death." It cannot be applied to large, moving, or inaccessible bodies of water.

3. A fly-trap devised by M. Bourgault du Cordroy for Stomoxys could well be adapted for the relief of stock from tabanids. The trap is simple and inexpensive, and the results are said to be effective and rapid. It consists of:

a. A darkened, partitioned building, with entrance and exit doors.

b. A brush of leaves and branches.

c. A lighted chamber into which the flies are attracted and where they are trapped and destroyed.

The building is erected at a convenient place in the pasture land, and the herd is passed single file through the brush. After the first day, the cattle are said to go at a gallop to the trap to free themselves of the flies. A black, tailless, animal may be used as a decoy for the flies, and when a number of flies have collected on its body it is passed through the brush.

This trap, while its effectiveness is highly praised, can only be constructed on large cattle-raising ranches. Its cost would be prohibitive for the small-scale breeder or individual farmer.

4. The harassed animals themselves seek relief from the flies. Congregating during the most annoying hours of the day in groups, they seek protection in the shade of trees, and in the shelter of open sheds.

Horses and oxen at work are covered with hoods of burlap or nets over the head and neck. Holes are cut in the hoods for the eyes, ears, and nostrils.

5. Drainage of swamps and marshes, clearing and cultivating these areas, is the only radical measure that would conduce to a substantial eradication of most of the horseflies. It would cut off their breeding beds and the moisture necessary for development.

The difficulties connected with a large-scale measure of this kind are obvious.

HABITS

1. Food habits:

The larvæ of Chrysops subsist on the organic matter that is found in their habitat in soil, slime or decaying leaves. In the laboratory they thrive in a medium rich in decayed organic matter. They are never tempted by animal food even when no other food is given. The larvæ devour the soil and extract whatever organic matter there may be in it, much after the fashion of earthworms. Unlike the Tabanus larvæ *Chrysops larvæ* are not cannibalistic. Stammer (1924) kept five larvæ in the same dish for four weeks, and they did not attack one another although no other animal food was given. The stomach contents consisted entirely of the fine slime in which he reared them. We kept larvæ of *Chrysops indus* and *Chrysops obsoletus* and never noticed any case of cannibalism. In nature they are usually found in aggregations in a small space, while the cannibalistic Tabanus larvæ are widely disseminated in the soil.

Some investigators found that the larvæ of *Chrysops callidus* were carnivorous and cannibalistic at least during the early instars. We could not verify this tendency in the two species reared by us.

Jones and Bradley were unsuccessful in their attempts to rear tabanid larvæ in nutrient agar. These investigators also observed that the larvæ feed very little during cool days.

The adult female is blood-sucking, while the male subsists on nectar from flowers and plant juices. But while the male has never been observed to bite animals, the females visit flowers, extract juices of fruit and sap of trees when no animal food is obtainable. They are found in abundance in regions where large mammals are scarce, and where they could hardly satisfy their thirst for blood. The presence or absence of the flies in the Alps

is said to be wholly conditioned by climatic and topographic factors, and very slightly by the presence or absence of cattle. Sometimes a coat of pollen is found on the bodies of female specimens collected in the field.

One is led to believe that these flies were originally zoophagous in both sexes. The hoematophagy of the female and the phytophagy of the male are secondary developments. Zoophagy is still preserved in the larvæ to some degree, while in the adult female, due to the fact that the prey attacked is too large to be devoured totally, hoematophagy, which is a convergent of zoophogy, was adopted. The phytophagous habit is a later adaptation to which the males are adjusted by the morphological changes in the feeding apparatus, and the female is still in the process of adjustment.

2. Drinking.

In the discussion on control reference has been made to the peculiar habit of *Tabanidæ* in visiting bodies of water. The purpose is not known; it may be for drinking. Both sexes are frequently observed hovering over the water, lowering themselves at intervals to the surface, and dipping the proboscis in the water. At the time the ventral surface of the body is in contact with the surface of the water.

3. Flight.

While the buzzing of the larger tabanids is recognized from a distance, the quiet flight of the deer-flies is hardly heard. They circle around the head and suddenly disappear. They are rapid fliers and are said to follow trains or cars for long distances. They are especially attracted by dark and moving objects.

4. Bite.

The place of biting is peculiar to every species. I noticed that *Chrysops obsoletus* prefers the exposed part of the hand, while *Chrysops indus* bites on the back of the neck. When the fly alights on its victim it explores a small area with the labella prior to piercing the skin. In order to get blood the mandibles must pierce through the epidermis. The prick is felt distinctly, but no pain is experienced while the fly is ingorgating. After a

complete meal which lasts about 10 minutes the walls of the gut of the fly are greatly stretched. The blood goes directly to the stomach where it is present as a fluid. This suggests the presence of an anti-coagulin secreted by the salivary glands which prevents the coagulation of the blood. There is no reservoir for the blood in the crop as is the case in the tsetse flies. The crop contains a watery, colorless fluid which is believed to be saliva as in the cockroach, or juices obtained from the surface of plants as in mosquitoes.

Veil and gloves are necessary as protection from bites of Chrysops in the Florida Everglades. They penetrate heavy flannel army shirts and riding breeches.

An interesting problem is presented by the fact that the number of larvæ of a particular species is not found in the same proportion as the adults of that species in a locality. Cameron found the proportion to exist in the northern regions of Canada, but Webb and Wells could not find such correlation to exist in Antelope Valley, and Philips (1926) found conditions in Minnesota which point to the fact that the most abundant species of larvæ were least represented as adults. Snyder (1917) was unable to find any great number of larvæ or exvuiea in the Everglades of Florida where the adults are extremely numerous. The banks of the three lakes in Durand-Eastman Park yield very few larvæ of *Chrysops indus,* while the adults of this species are dominating the Park in the Summer. Upon discussing this matter with Dr. J. D. Hood, he called my attention to a similar condition existing in the case of some dragonflies where the adults are found far from the habitat of the larvæ. The explanation was offered that this is done for economy in food supply. This may also be true for *Tabanidæ.*

BREEDING METHODS

The egg mass found in the field is carried into the laboratory with the plant on which it is fixed, and placed in its natural position in a dish or bottle containing some water on its bottom. As soon as the larvæ hatch they are drawn out of the water by a pipette and placed into dishes containing wet sand or water-soaked dead leaves. After the first molting they are transferred

into permanent vessels in which natural conditions of habitat are simulated.

The breeding of Chrysops larvæ is much easier and simpler than that of the carnivorous and cannibalistic Tabanus larvæ. They are saprophogous and hence a layer of soil rich in decayed organic matter, kept moist, will provide sufficient nourishment. They are not cannibalistic and therefore can be reared in groups without the necessity of individual care.

The methods employed by the various investigators differ according to locality and purpose. The early workers used boxes or glass jars containing damp earth and decayed organic material. This medium while it simulates closely natural habitat is not convenient for observation on the activities of the larvæ, habits of feeding, and for keeping records of ecdysis and growth. Modifications of this method were used by Hart, Hine and others.

Issaac (1914), working in India, used clean sand instead of earth. The early instars were kept in small beakers, and the older larvæ were transferred into jelly jars. The sand was kept moist all the time, and the jars were covered with gauze and petri dishes to prevent escaping. The sand layer was tilted to allow a moisture gradient. Before observation, an excess of water was added to each jar or beaker and the contents shaken gently. This brought to the surface the larvæ, cast skins, food material, and refuse. After all observations were completed, measurements made, and waste material cleaned, the sand was again allowed to settle by tilting the vessel on one side, the excess of water poured off, and the larvæ allowed to burrow in the sand. Issaac was the first to record on the number of larval instars.

Stammer (1924), in Germany, reared his Chrysops larvæ in glass dishes filled with moist sand and slime. The dishes were covered with heavy lids to prevent escape.

Patten and Cragg in India, reared large numbers of tabanids in trays of galvanized iron about six inches deep. The trays were filled with sand and mud sloped off to simulate the shore of a stream or pond. Water plants were planted in the mud and the trays were always kept about three-fourths filled with water, preferably from a stream. The water was changed every ten days through a hole bored in the bottom of the tray, near one

corner and stopped with a cork. The egg masses were collected and as soon as they hatched the young larvæ were transferred into the trays. The vessels were stocked with earthworms and decayed organic matter. When mature, the larvæ were removed from the trays and placed in jars with mud. The mature larvæ burrowed into the mud and pupated just under the surface. The pupæ were then placed in cages covered with mosquito netting.

The cages contained iron trays filled with mud. Holes were made in the mud and the pupa placed in them. The netting was stretched over a framework of iron rods to allow penetration of sunshine and to prevent the escape of the emerging adults.

Mitzmain, working in the Philippines on *Tabanus striatus,* reared the flies in a capacious fly-proof building with brass gauze sides and top, and cement floor. The building was sufficient to house four or six animals and thousands of flies. The building contained a concrete water tank with plants growing in it.

For breeding on the work-table in the laboratory a simple and convenient method has been developed. It is based on the realization that the chief responses of the larvæ are: (a) negative phototropism, and (b) positive thigmotropism.

The larvæ will thrive in any surroundings where these two responses are satisfied. For this purpose glass vials or test tubes that are laid out with strips of filter paper or ordinary paper toweling are used. The paper is kept moist to substitute for the damp mud. It affords opportunities for contact of the body with something, and a medium to hide in. The vials are covered with pieces of cheese cloth and tied around with rubber bands to prevent escape and at the same time to keep down evaporation and allow plenty of fresh air. The pupæ are transferred into jars or trays with mud.

In our work we used flat glass dishes with sand and decayed leaves, as well as vials with filter paper. Both proved to be satisfactory.

COLLECTING CHRYSOPS LARVÆ

Chrysops larvæ can be collected at all times of the year in mud and soil above the water level and near the edge of any permanent body of water. They are usually found about two inches underground, and several ways of obtaining them are suggested.

When only a few specimens are desired, the procedure is to wade into the water along a steep margin and to loosen the soil by means of a garden hand fork or horticultural hand weeder. A handful of water is poured over the loosened soil and the larvæ will show up on the surface.

Another method is straining the mud through an ordinary wire kitchen-sieve. A lump of mud is taken from the edge of the water and placed in the sieve. The sieve is immersed in the water and gently shaken. The dirt is washed through the wire meshes and the larvæ soon show up clinging to grass roots or weeds.

But these methods of collecting are obviously not suitable for cold winter days. The process would also be impracticable when larger quantities of larvæ are desired. In such cases other methods have been suggested.

The mud is brought to the laboratory in a tin container. Water is added to form a thin, muddy fluid which is stirred gently and passed through a sieve. The larvæ are caught in the mesh of the sieve.

We followed the methods of Stammer. Blocks of mud which were dug up in the field were brought into the laboratory and spread over a screen wire laid over a basin with some water on the bottom. The larger larvæ were noticed while the mud was being broken, and those not picked up in this way dropped into the water as soon as the layers of mud dried.

The larvæ are differentiated from other dipterous larvæ in the same habitat by: (1) prominent, downward projecting mandibles, (2) glossy sheen of the integument, and (3) sub-cylindrical form of the body with rings of projecting forelegs on the abdomen.

MATING AND OVIPOSITION

In the early hours of a summer day, usually before sunrise, the sexes of Chrysops species in common with other *Tabanidæ* gather at their "meeting places" on the hill summits or in the foliage of trees near water, where copulation takes place. Mating has been observed at rest and on the wing.

Oviposition is stimulated by the presence of water and by vegetation overhanging or projecting out of the water. Eggs were

never found on stones and wood or away from the water. As a rule oviposition takes place in the morning, but it has also been observed in the afternoon hours of warm days in June and July. The process occupies about half an hour. The fly is very sluggish during that time and is not easily disturbed. Hine (1906) carried a fly with the leaf, on which she was ovipositing, into the laboratory, took a picture, and made detailed observations of the act, while the fly continued to lay the eggs apparently undisturbed. The great number of unfinished egg masses found in the field would indicate, however, that they readily leave off in the middle of the act. A female of *Chrysops moerens* continued ovipositing while I watched closely for about 20 minutes, turning the blade of the sedge several times. But she suddenly fled without any cause, leaving the mass unfinished. The place on the leaf, kind of plant, and the distance from the ground do not seem to have any specific significance. The process of ovipositing was first described by Hine and later also by Cameron and other investigators. The process in brief, as observed by the author in *C. indus,* on cat-tail, is thus:

The female alights on the leaf head downwards and moves around feeling the surface with the tip of the abdomen before starting to lay the first egg. Then the tip of the abdomen is recurved anterio-ventrally beneath the abdomen. A protruding egg is glued to the surface of the leaf and the abdomen is then brought back to the normal position. This frees the egg. By repeating these movements more eggs are deposited on both sides of the first egg in single, oblique rows until a mass of from 100 to 300 eggs is formed in a single layer. Each egg is brushed lightly by the ovipositor as it is laid. Before laying a new egg the preceding egg is touched lightly, probably for the purpose of orientation. Each egg is laid so as to overlap its predecessor, leaving only about one-third of it exposed. The eggs are glued to one another and to the surface of the leaf by a secretion. The whole mass is then covered by a thin, water-proof, insoluble, protective membrane. The egg mass presents a flattened, elongate, gray or creamy-white spot, tapering at both ends or, when unfinished, the lower end is truncate.

The mass is grayish when freshly laid, but gradually gets darker until it becames brown or lustrous black in color. The darkening is quicker when exposed to sunlight.

THE EGG

The individual egg is semitransparent and contains a whitish mass of yolk in its upper third. It is cylindrical in form with rounded ends. Only about one-third of each egg is visible at the surface of the mass, the rest being covered by the following egg which obliquely overlaps it. The egg is about 1.5 mm. in length, and about .25 mm. in diameter. It is straight or slightly curved, broader in the middle and gradually narrowing toward the ends.

The eggs are believed to be laid soon after fertilization, for in sections made of these eggs no great development was observable. A blood meal is essential to the maturation of the eggs. The duration of the egg stage depends upon the temperature. It varies from five days in sunshine to seven days when kept in the shade.

The eggs of a single mass hatch in nearly the same time, and the young larvæ leave through a slit in the chorion at the upper pole of the egg. The egg-cluster at that time presents a wriggling whitish mass. The larvæ are very active and crawl one upon the other, clinging together, and presenting moving lumps which soon loose their hold upon the black egg-shells and drop into the water. The lumps sink to the bottom and the larvæ separate, each burrowing into the sand or mud, after molting.

THE LARVÆ

The larvæ ecologically belong to the hydrophytic area. From hatching to the approach of cold days the larvæ feed and grow. They become dormant and stop feeding late in the fall when they burrow deeper into the soil. They resume feeding in spring and are found full-grown in April and May.

The full-grown *Chrysops* larva is 10–15 mm. long and 1–3 mm. wide. The body is yellowish white or light brown in color, sometimes with a greenish tinge, with pale or brown pubescence. The integument is transparent and shiny, due to the longitudinal striae of the chitin.

The head capsule, usually darker than the body, is small and can be completely telescoped into the thorax. The mandibles are dark in color and slightly curved ventrally. The antennæ are distinct and composed of three joints; basal joint small, the others of varying length. The apical joint is bifid. The ocelli are dorsal in position, and consist of a single, dark, irregular optic spot on either side of the head capsule.

The thorax is composed of three distinct segments with a dark girdle of pubescence of varying width on the anterior margin of each segment, and a pair of ventral bristles. The thorax bears a pair of spiracles which are situated laterally in the boundary line between the prothorax and the mesothorax.

The abdomen consists of eight segments, the last being modified into an anus and a respiratory syphon (Cameron considers the syphon as a separate segment, the ninth). Segments 1–7 are capable of being slightly telescoped into one another when in motion. Each segment usually bears an anterior dorsal band of pubescence and rarely also a posterior ring of pubescence. Each of the abdominal segments, 1–7, possess a pair of transverse fused dorsal prolegs, a pair of distinct strong lateral prolegs, and a pair of rounded ventral prolegs. The prolegs are situated on the anterior portion of each segment and present a heavily chitinized ridge circling around the segment. The lateral and ventral prolegs bear rows of recurved setæ which aid in locomotion through the relatively compact soil.

The anal segment is longer than the preceding segments, terminating in a short subconical syphon which is capable of retraction and extension. Several dark spots of pubescence on the anal segment are of use in classification. The syphon bears a dorsal spiracle in which the two tracheal trunks terminate. The spiracle is in the form of a protrusile spine or in the form of a vertical slit. This is used by the mature larvæ to break the surface film of the water for the exchange of air when they are submerged.

The larvæ are metapneustic, the first, prothoracic pair of spiracles being non-functional. Two main tracheal trunks of a shining silvery color are conspicously visible through the transparent integument. They run all the length of the body, parallel at their anterior portion, and coiled in the sixth and seventh abdominal segments, coming in contact again in the syphon.

The intestines usually show through the integument, as filled with a colored fluid, depending on the food. The dorsal blood vessel and the coiled Malpighian tubules are also seen through the chitin.

A unique structure in the larvæ of Tabanidæ is the organ discovered by Graber in 1878 and called Graber's organ. It is situated on the dorsal side of the anal segment between the two tracheal trunks. It is the structure that attracts immediate attention with its black, oscillating bodies in the living specimen. The organ consists of the following parts:

1. The principal chitinous sac.
2. Smaller, secondary, chitinous capsules enclosed within the principal sac.
3. Black globular bodies suspended in the fluid filling the capsules.
4. A muscular mechanism by which the organ is moved pendulum-like when the larva is in motion, and
5. Nerve attachments and membranes to maintain the position of the black bodies.

The entire organ is piroform in shape. The wider fundus tapers gradually to a slender thread-like tube which opens dorsally in the furrow between the anus and the syphon. The organ according to Cameron is probably an invagination of the integument and the black bodies are modified cuticular hair.

When the body is at rest the organ is practically stationary, but with the slightest movement the suspended black bodies begin their lateral oscillations. The number of the black bodies is variable in the various species. Only the principle sac is functional. The other smaller capsules within it are remains of the sacs of the earlier instars which persist after molts. New black bodies appear after each molt, but the old ones remain unfunctional in the capsule all through the larval stage. In some mature larvæ the number and the arrangement of the black bodies is constant enough to warrant their use in classifications. In *Chrysops* larvæ there are usually four pairs of black bodies, and only those suspended from the anterior wall of the main capsule are functioning.

The function of the organ has been interpreted by many workers.

1. *Auditory.* Graber who studied the organ in detail, in 1882, believed it to be for the purpose of hearing. The sac, accordingly, would be an otocyst and the black bodies, otholiths. The difficulty with this view is the apparent uselessness of an auditory organ for a larva living underground.

2. *Glandular.* Lecaillon (1906) denies any sensory function to the organ and would rather assign to it a glandular function, that of secreting pigment.

3. *Sound-producing.* Paoli (1907) believes that Graber's organ is responsible for the clicking noise produced by some of the larger tabanid larvæ. It has been pointed out since then that the noise is caused by the telescoping of the segments of the abdomen during locomotion.

4. *Static.* The function assigned to the organ by Cameron (1926), and which is generally accepted, is that of maintaining the equilibrium and orientation of the body. The black globular bodies accordingly assume the role of sensory hair which are stimulated by the movements of the fluid in the capsule when the larva is in motion. The impulses are transmitted through the nerve attachments to the ganglia of the central nervous system. They are then conveyed to the muscles of the body causing them to perform coordination contractions by which equilibrium and orientation of the organism is effected.

THE PUPA

Late in April and in May the full grown larvæ of *Chrysops* move nearer toward the surface for pupation. The larvæ become sluggish and stop feeding entirely. They enter the pre-pupal period which lasts from one to two days prior to pupation.

This stage is characterized by:

1. The transformation of the prothoracic spiracles into white, slender tubes projecting laterally and anteriorly at the base of the prothorax. Respiration during the prepupal stage is amphipneustic.

2. Partial retraction of the head.

3. Slight swelling of the prothorax.

4. The initial development of the external features of the pupa that can be seen through the integument of the larval skin.

The pupa emerges out of the larval skin by pressing forward and causing a longitudinal split on a mid-dorsal line of the thorax. The head is freed first and the exuvium is then pushed backwards by contractions and expansions of the abdomen, assisted by the fringes of pupal bristles on the abdominal segments. The pupa usually lies in an erect position in compact soil above the water level.

Chrysops pupæ are brownish-yellow in color and measure from 10–15 mm. in length, and 2–3 mm. in diameter. The head and the thorax are fused. Short antennæ overlie the eyes; and the space between them is variously cleft and furrowed with ridges of chitin.

The thoracic spiracles projected in the pre-pupal stage are now flattened and extend out dorsally. The wing pads are short, barely reaching the second abdominal segment.

Abdominal segments 2–7 are distinctly divided into dorsal, lateral, and ventral areas. Each lateral area bears a spiracle. A comb of dorso-lateral pupal spines surround each abdominal segment, except the first, on the posterior margin. The anal segment bears six sharp projections on its posterior end. These form the pupal aster, which consists of three pair of projections: one pair directed dorsally, a larger dorso-lateral pair, and a ventro-posterior pair. Each projection terminates in sharp, recurved hooks.

The pre-anal fringe and sometimes the aster offer a means of distinguishing the sexes. In the pre-anal fringe of males the bristles are of equal size; in females the row is broken in the middle. The anal region is, generally more protuberant in males than in females. The size and strength of the astral hooks differ in the sexes.

The pupal period is of varying duration, ranging from five days in the field to two weeks in the laboratory.

An interesting case of pupal adaptation has been reported by Lamborn (1929) from Nyasaland. It concerns the ability of the pupa to survive in dry mud.

The writer noticed smooth discs at the intersection of the cracks in the dry mud about the size of a penny, in a hollow which served to collect water in the rainy season. These discs were

slightly concave and perfectly circular with an opening about the diameter of a lead pencil in the center. Each disc proved to be the top of a cylinder of mud about $3\frac{1}{2}$ inches in height which could be readily removed from the ground. Inside of each cylinder was found a pupa or a pupal shell.

The cylinders were presumably constructed by the larvæ when the mud was plastic by spiral movements. With the drying of the upper layers of the mud during the dry season the larvæ moved gradually downward where the moisture was still present. At the desired depth the larvæ burrowed in the mud to pupate, sealing the entrance to the cylinder. When ready to emerge the pupa breaks through the seal of the cylinder by the aid of the pupal armaments on the head, and the imago escapes.

The cylinders then serve:

1. To protect the larvæ from sudden exposure to heat when the cracking of the mud takes place,
2. To allow the pupa to move up and down so as to escape the heat during midday hours,
3. To retain moisture, necessary for the organism, and
4. To protect against attack of enemies.

THE ADULTS

Toward the end of the pupal period the pupa moves toward the surface with the aid of the fringes and aster, ready for emergence of the adult. This is accomplished by a slit in the dorsum of the thorax and by breaking the plate of chitin covering the head. The adult on emergence remains motionless for about half an hour, clinging to blades of grass near the deserted pupa-case. They are then in the teneral stage. The wings at that stage are much shorter than the enlarged abdomen. After the emission of a yellowish mecomium through the anus, and the stretching of the wings, the fly attempts to take wing for short distances.

The adults are on wing from May to August, the season of greatest activities being July and August. The span of life of the female is longer than that of the male.

The life cycle of *Chrysops* is believed to be one year. The difference in size often found in larvæ of the same species may be due to food and to differences in time of hatching, since the egg-laying season stretches over a period of over two months.

The one-year life cycle can be summarized thus: Incubation, about 1 week; Larval period, about 10 months; Pupation, from 1 to 2 weeks; Imago, about 2 months.

KEYS TO THE IMMATURE STAGES OF CHRYSOPS

The immature stages of *Chrysops* can be distinguished from other New York *Tabanidæ* by the aid of the following keys:

EGGS

(After Hart)

1. Arranged in a single tier lying flat on the surface of the object, and overlapping one another upwards; egg mass forming an oval or diamond-shaped area at one or both ends ..... *Chrysops*
– Laid at an angle to the surface on which it is deposited, in more than one tier 2
2. Creamy white at the time of hatching ..... *Goniops*
– Dark brown or black at time of hatching ..... *Tabanus*

LARVÆ

1. Body club-shaped, thoracic segment slender, abdominal segments robust ..... *Goniops*
– Body tapering anteriorly and posteriorly, not club-shaped 2
2. Apical antennal segment much longer than the preceding segment, usually bifid; diameter of main trachial trunks the same over the entire length; dorsum of thoracic segments nearly as striated as those of abdominal segments. Small size. Range between 10–15 mm. ..... *Chrysops*
– Apical antennal segment not larger than the preceding segment; diameter of main tracheal trunks more inflated in the posterior part of the body than in the anterior; dorsum of thoracic area nearly free from striæ. Large size. Range when mature, between 15–50 mm. ..... *Tabanus*

PUPÆ

1. One spine on each side of median line on dorsum of each abdominal segment much stronger than the others in the series ..... *Goniops*
– Spines of each series almost of a uniform strength 2
2. Antennæ surpassing adjacent margins of head, about twice as long as the width at the base, bristles on frontal tubercles double; abdominal spiracles slender, subcylindrical near apex. Small size, range between 10 to 15 mm. ..... *Chrysops*
– Antennæ not projecting beyond lateral margin of head; length about equal the basal width; frontal bristles single; abdominal spiracles subconical or rounded; of medium or large size, range between 15–35 mm. ..... *Tabanus*

KEY TO THE ADULTS OF CHRYSOPS

(After Hine)

Chrysops may be distinguished from the other genera of *Tabanidæ* commonly occurring in New York by the aid of the following key:

A. Hind tibiæ with spurs at tip.
  B. Third segment of antennæ composed of eight rings, the first of which is only a little longer than the following ones.....
    C. Front of female narrow; ocelli present or absent; fourth posterior cell at least open .....*Pangonia*
    CC. Front of female broad with a large denuded callus; ocelli present; wings in both sexes with a dark picture.....*Goniops*
  BB. Third segment of antennæ composed of only five rings, the first of which is much longer than the following ones. Second segment as long or but little shorter than the first; eyes in life with green patches .....*Chrysops*
AA. Hind tibiæ without spurs at tip; third segment of antennæ with a well developed basal process .....*Tabanus*

KEY TO THE NEW YORK SPECIES OF CHRYSOPS

(After Kröber)

1. Apical spot and cross-band of the wing completely fusing together, and occupying the entire apical part, except for a circular hyaline area in the region of the first submarginal cell .....Group I *bistellatus*
– Apical spot, when present, distinctly separated from the cross-band by a hyaline triangle on the posterior margin of the wing.....2
2. Wings without apical spot, or represented by a faint shading on the apex of the wing. Cross-band not quite reaching the posterior margin of the wing, leaving at least a fine hyaline border in the distal end of the fourth posterior marginal cell .....Group II *excitans*
– Wings with a distinct apical spot 3
3. Antennal joint 3 shorter than joint 2 .....Group III *ceras*
– Antennal joint 3 longer than 2 4
4. Antennal joint 1, or 1 and 2, thickened or club-shaped. Group IV *virgulatus*
– Antennal joints cylindrical, slender 5
5. Both basal cells of wing hyaline, or with only a small band of infuscation at their very tips, the area of infuscation never exceeding the clear area in the cells .....Group V *callidus*
– Area of infuscation in the first basal cell greater than the clear area, or the cell is entirely filled with brown .....Group VI *vittatus*

Of the six groups constructed by Kröber for the Chrysops species of North America, I is not represented in the New York insect fauna, but has been recorded from New Jersey (*Chrysops bistellatus* Daecke, Ent. News, XVI, p. 249, 1905). Group II is represented in New York by eight species; Group III contains only two species, both from Mexico; Group IV includes six species, of which one, *brunneus*, is found over the entire area east

of the Rocky Mountains; the other five species being confined to Mexico and the Pacific Group. Groups V and VI are represented in New York by 12 and 9 species respectively.

Group I. *Bistellatus*

Abdomen yellow with two dorsal longitudinal stripes. Wings infuscated on the apical half, with a hyaline quadrate in the first submarginal cell ..... *bistellatus* Daecke

Group II. *Excitans*

A. Abdomen entirely black without any light marking.
  B. Cross-band on wing faintly outlined, obscure beyond the discal cell. Basal cells clear ..... *nigribimbo* Whitn.
  BB. Not as above.
    C. Cross-band distinctly dark-brown, nearly reaching the posterior margin in the fourth posterior cell. Basal cells brown.
      —Pleura on thorax with thick reddish-yellow tufts of hair. *celer* O.S.
      —Pleura with tufts of gray hair ..... *niger* Macq.
      D. Fifth posterior cell with circular hyaline spot at base. *carbonarius* Walk.
      DD. Fifth posterior cell brown at base ..... *mitis* O.S.
AA. Abdomen with gray or yellow markings, or triangular median spots.
  E. Cross-band very distinct, light or dark-brown.
    F. Abdominal segments with narrow, gray posterior borders; yellow lateral spots small ..... *sordidus* O.S.
    FF. Abdomen without gray posterior margins of segments. Yellow lateral spots large. Tergite 2 with yellow median triangle ..... *excitans* Walk.
  EE. Cross-band not distinct, pale brown, interrupted below the discal cell. Second tergite without gray or yellow triangle at middle, black with gray lateral spots ..... *cuclux* Whitn.

Chrysops carbonarius Walk.

(*Chrysops carbonarius* Walker. List of Diptera, British Museum I: 203, 1848.)

Length 8.5–9.5 mm. Antennæ 2–2.2 mm., wings 8–8.5 mm. long, 2.5–3 mm. wide.

Female. General body color black with a gray silky pubescence. Wings hyaline with a dark brown picture.

Head:—Face covered with yellow pollen. Callosities shining black. Frontal callosity rectangular with a sharp tapering point

reaching the large, dark, ocellar area on which are situated three reddish ocelli. Antennæ slender: joint 1 light brown, joint 2 reddish brown, furrowed; both joints with thick short black bristles. Joint 3 black, style indistinctly annulated. Front and vertex clothed with black hair.

Thorax:—Shining black, thickly clothed with delicate whitish hair. A row of long black hair on the sides of the thorax extend from the base of the thorax to the base of the wings. Pleura with three conspicuous white tufts of hair, the one near the base of the wing particularly thick. Near the base of the thorax is a circular area of a lighter hue, and on the sides are round light patches. Legs black, metatarsi reddish brown. Pubescence short, black, with rows of longer whitish hair on the inner side of the femora.

Wings infuscated at the base, in the costal and subcostal cells, over the proximal halves of the two basal cells. Cross-band covers the proximal halves of the marginal, first submarginal and first posterior cells; touches upon the apex of the first basal cell and fills completely the discal cell. The posterior border extends over the proximal one-quarter of the second posterior and obliquely over the one-half of the third posterior cells; it nearly fills the fourth, and touches slightly on the base of the fifth posterior cell. The rest of the fifth posterior cell, the axillary cell, the anal cell, the apical halves of the two basal cells and the apex of the wing, hyaline.

Abdomen:—Black, with whitish hair on the posterior borders which tend to form median triangular patterns on tergites 2 to 4. Venter black clothed with the characteristic white hair.

Male. Similar to female.

Distribution:—Maine to Minnesota; Quebec to Colorado.

Synonyms:—*ater* Macquart, 1850; *fugax* Osten-Sacken, 1875.

Chrysops celer O.-S.

Chrysops celer Osten-Sacken, Memoirs Boston Society Natural History, II: 376, 1876.

Length 8.5–9 mm., antennæ 2.5–3 mm., wings 8.5–9 mm. long, 2.8–3.2 mm. wide.

Female. General body color lustrous black with a silky yellow pubescence. Thorax with two median bluish-gray longitudinal

stripes and tufts of long ferruginous hair on the sides. Wings hyaline with a dark brown picture.

Head:—Face covered with reddish yellow pollen. Callosities shining black. Ocellar area black and irregular in outline. Ocelli reddish brown. Front and vertex covered with pale yellow pollen and yellow hair. Antennæ long and slender, joint 1 ferruginous, darker at the tip; joint 2 slightly furrowed, dark on the outer sides and at the tip; both joints beset with strong black bristles; joint 3 reddish brown at the base, the rest of the joint and the curved annulated style black.

Thorax:—Thickly clothed with silky yellowish hair which on the pleura form very conspicuous tufts of reddish hair. Two longitudinal stropes of a bluish-gray color are discerned on the anterior, but hardly reach beyond the mid-dorsal line. Legs black; metatarsi of the middle and hind legs yellowish, pubescence black with a mixture of gray on the femora.

Wings infuscated at the base, in the costal and subcostal cells, over the proximal three-fourths of the two basal cells, and at the very base and apex of the anal cell. Cross-band intensely brown and with nearly parallel: it covers the proximal halves of the marginal and the first posterior cells, touches upon the apices of the two basal cells, fills completely the discal cell, the fourth and fifth posterior cells, and obliquely extends over the base of the second and the proximal half of the third posterior cells. A very narrow border of diffused infurcation separates the cross band from the inner margin of the wing. Apex of the wing, axillary cell, middle of basal cells and most of anal cell, hyaline.

Abdomen:—Tergites black with narrow light posterior borders and short grayish pubescence. Rudiments of median triangles are faintly outlined by silvery white hair on tergites two and three. Venter black with grayish hair, on the last sternite.

Male. Uniformly black. Pubescence black including the characteristic thick tufts on the pleura. Infurcation on the wings more intensely brown than in the female, and fills the entire anal cell as well as the greater part of the basal cells.

Distribution:—Long Island to Minnesota; Province of Quebec to Kansas.

Synonym:—*cincticornis* Walker, 1848.

Chrysops cuclux Whitn.

(*Chrysops cuclux* Whitney, Canadian Entomologist II: 35, 1889.)

Length 7.5–8 mm., antennæ 2.1–2.2 mm., wings 7–7.5 mm. long, 2.5–2.9 mm. wide.

Female. General body color lustrous black. Thorax with two rudimentary longitudinal grayish spots. Abdomen with faint reddish brown spots on the first and second tergites. Pubescence generally silky gray. Wings cloudy hyaline with a very pale brown picture.

Head:—Face covered with silky gray pollen. All callosities shining black. Ocellar area wide and black with three reddish brown ocelli. Front and vertex with long gray and silky gray pollen. Antennal joint 1 light brown, darker at the tip; joint 2 brown, deeply furrowed at the middle; both joints clothed with short black bristles. Basal part of joint 3 brownish, the rest of the joint and the short annulated style black with brownish hue.

Thorax:—On the anterior part of the dorsum are two grayish stripes which hardly reach one-third the length of the thorax. Pubescence delicate and gray; pleura with thick tufts of long gray hair. Legs black, the metatarsi of the middle and hind legs brown. Pubescence on all parts black, front femora with long grayish hair.

Wings infuscated at the base, in the costal and subcostal cells, and on the proximal two-thirds of the two basal cells. Cross-band follows a nearly straight line from the stigma towards the inner margin of the wing. It covers the upper halves of the marginal and submarginal cells, touches upon the apices of the two basal cells, fills completely the discal cell, extends over the proximal half of the first posterior, about one-third of the second and third posterior cells, and faintly shades the fourth and fifth posterior cells. Along the anal cell the brown fades into the grayish hyaline of the anal cell, the axillary cell and the apex of the wing.

Abdomen:—Clothed with a gray silky pubescence. Tergites 1 and 2 with lateral contiguous spots of a reddish brown color. The hair on these lighter areas are whiter and longer than the general pubescence of the tergites. Similar white hair tends to form median triangular patterns on tergites 2 to 4. Venter black, each sternite with a light posterior border. The gray hair is uniformly distributed and are longest on the last sternite.

Male unknown.

Distribution:—Maine to Minnesota; Quebec to Pennsylvania.

Synonyms: *cuchix,* Ricards, 1911.

Chrysops excitans Wlk.

(*Chrysops excitans* Walker, Diptera Saundersonia, or characters of undescribed insects in the collection of W. W. Saunders. Diptera I: 72, 1850.)

Female. Length 10.5–11.5 mm., antennæ 2.4–2.5 mm., wings, 9.5–10 mm. long, 3–3.5 mm. wide. General body color black. Thorax with faint greenish longitudinal stripes. Abdomen with yellowish median and lateral spots. Wings hyaline with a light brown picture.

Head:—Face covered with pale yellow pollen. All callosities shining black. Front and vertex beset with long grayish hair, particularly thick on the ocellar area. Antennal joint 1 reddish yellow, gradually turning dark towards the tip; joint 2 dark brown on the outer side, yellowish on the inner side, furrowed. Both joints covered with thick black bristles. Joint 3 longer than 1 and 2, with a short style on which four annuli can be distinctly seen.

Thorax:—Lustrous black with two greenish longitudinal stripes, separated by a median narrow purplish line. The stripes are bordered on their outer sides by a reddish longitudinal stripe which does not reach the mid-dorsum. Pubescence reddish-yellow, which on the pleura forms thick turfts of hair particularly long at the base of the wings. Legs black with a yellow tinge on the femora.

Wings infuscated at the base and in the costal and subcostal cells, over the proximal three-fourths of the two basal cells, and at the very base of the anal cell. The cross-band is comparatively narrow and undulating; it covers the proximal halves of the marginal, first submarginal and first posterior cells; touches the very apices of the two basal cells and fills the entire discal cell; it extends over the proximal one-fourth of the second and third posterior cells, faintly fills the fourth and the proximal half of the fifth posterior cells, and tinges the apex of the anal cell. Apex of wing, axillary cell and a border on the inner margin of the wing hyaline.

Abdomen :—Tergite 1 black with a light posterior border which forms a median crescent-shaped spot, with its gray hair very distinct from the surrounding black pubescence. On either side is a reddish yellow spot of varying patterns. Tergite 2 with a light posterior border which broadens into a triangular median spot, the apex nearly reaching the middle of the tergite. Two lateral spots similar to those on tergite 1 and contiguous with them. Tergites 3 to 6 black with light posterior borders and rudiments of median spots indicated by gray hair more delicate and longer than the general black pubescence.

Male. Similar to female in most characteristics. Abdomen lacks the triangular and lateral spots. Picture of the wing more intensely brown than in the female.

Distribution :—Maine to Minnesota; Ontario to District of Columbia.

(*To be concluded*)